THE EQUILIBRIUM FUNCTION OF THE OTOLITH ORGANS OF THE THORNBACK RAY (*RAJA CLAVATA*)

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During the oscillographic study of the mode of function of the semicircular canals of the ray (Lowenstein & Sand, 1940*a*, *b*), it became clear that the accessibility of the elasmobranch labyrinth and the satisfactory survival of preparations of the labyrinth in the isolated otic capsule opened up the possibility of an extension of the work to the otolith organs in the utriculus, sacculus and lagena. This has now been carried out in experiments described in the present paper.

METHODS

Male and female rays of a wing span of 15–24 in. were killed by decapitation, pithing, and removal of the brain. The cranium was then isolated and the labyrinth approached through the cartilage at the back of the orbit or from the ventral side. Text-fig. 1 shows a ventro-lateral view of the membranous labyrinth after a maximum exposure of the otolith organs. Openings into the peri-lymphatic space of a much smaller extent were made for the exposure of individual receptors. In the case of the utriculus the approach was made from the orbit, and nerve twigs from the utricular nerve fan were cut at its proximal end and peeled up towards the lateral margin of the macula. The ampullary nerve branches supplying the anterior vertical and horizontal canals were divided in order to avoid the intrusion of spurious ampullary discharges.

In the case of the ramus inferior the posterior ampullary nerve is well out of the way, and the sacculus can thus be isolated by transection of the free-running branch supplying the lagena. The latter is fortunately long enough to allow isolated pure lagena twigs to be peeled off for electrical pick-up. A choice of the region of the sacculus macula to be recorded from was possible owing to the convenient fanning out of the saccular branches of the ramus inferior. Very small twigs could be isolated which, as a rule, contained only a few functional units, the number of which could be further reduced, often to a single functional fibre, by careful crushing of the twig or by its further subdivision by splitting.

When the desired twig had been prepared it was picked up in a silver-plated forceps electrode, held in position by a number of rods connected to the preparation holder by rotary clamps. The second electrode was applied to some inner part of the cranium. The holder was then clamped to a tilting device (Text-fig. 2) with the 'nose' pointing in any desired direction. The apparatus was designed for tilting movements about any horizontal axis desired, smoothness of movement and constancy of speed being assured by the use of a 50:1 reduction gear operated by hand. The wheel at the left was graduated into 360 degrees for the accurate reading of the tilting angle. The slotted
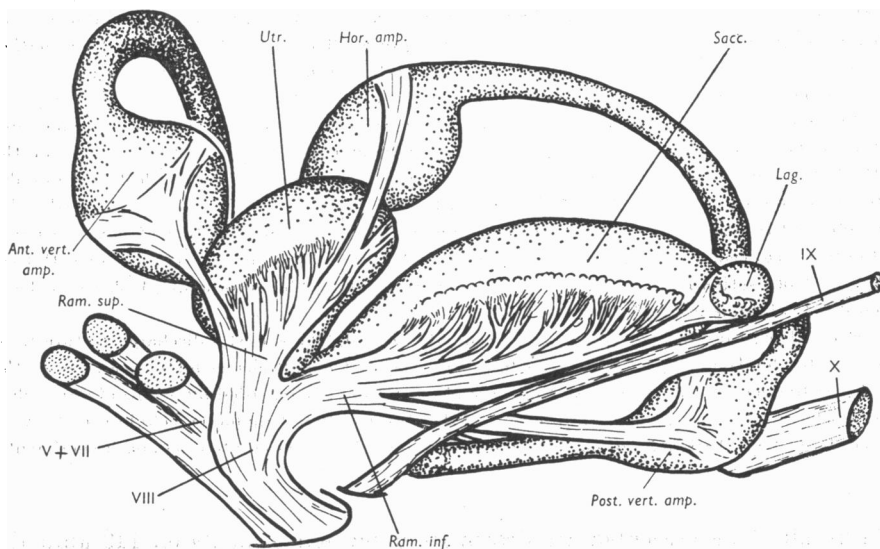
Text-fig. 1. Ventro-lateral view of the membranous labyrinth of the ray. *Ant. vert. amp.* =anterior vertical ampulla; *Hor. amp.* =horizontal ampulla; *Lag.* =lagena; *Post. vert. amp.* =posterior vertical ampulla; *Ram. inf.* =ramus inferior; *Ram. sup.* =ramus superior; *Sacc.* =sacculus; *Utr.* =utriculus; V–X =5th–10th cranial nerves.
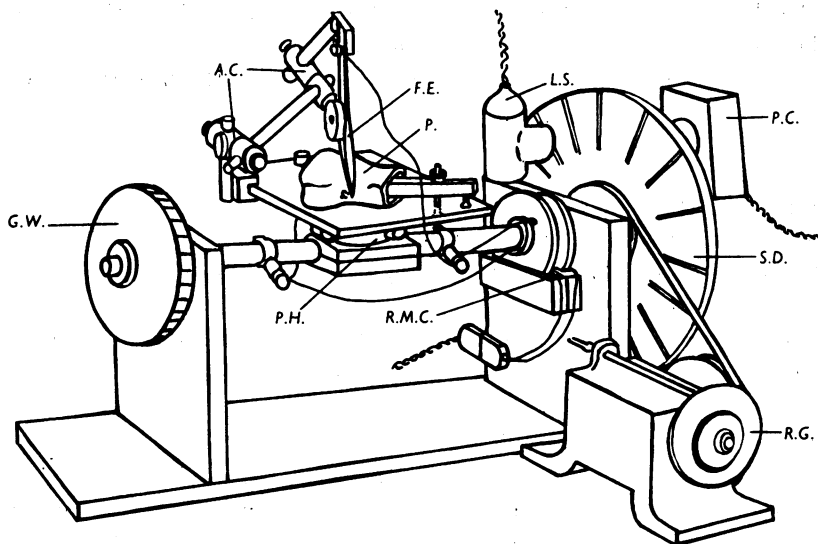
Text-fig. 2. Diagram of tilting device. *A.C.* =angle clamps; *F.E.* =forceps electrode; *G.W.* = graduated wheel; *L.S.* =light source; *P.* =preparation (posterior half of cranium); *P.C.* = photoelectric cell; *P.H.* =preparation holder; *R.G.* =reduction gear; *R.M.C.* =rotary mercury contacts; *S.D.* =slotted disk.

disk at the right was made to intercept a light beam focused on a photoelectric cell which, through a relay, switched a lamp in front of the camera serving as a rotation signal for the film records. This signal gave a flash of light for every three degrees tilt and, together with a time marker (24/sec.), made possible the recording of extent, acceleration, and speed of tilting of the preparation during experiments. The preparation holder was connected with the input of a high-gain balanced resistance-capacity coupled amplifier and cathode-ray oscillograph by means of two rotary mercury contacts which worked satisfactorily without producing electrical artefacts. Apart from the cathode-ray oscillograph and the usual monitor loudspeaker, we also used an electronic impulse integrator or rate counter which enabled us to take continuous readings on a calibrated milli-ammeter of the rate of impulse discharge at any given moment. The advantage of this device was not only a great economy in recording film, but also the possibility of using preparations with two, three, or more active units for quantitative response analysis, film records of which would have been practically unanalysable.

Yet another recording device proved exceedingly helpful. The acoustic discharge picture from the monitor loudspeaker, readings of rotation angles, and simultaneous meter readings of the discharge frequency from the preparation were phonographically recorded by means of a recorder-play-back set obtained from Government Surplus Stores. Small diameter cellulose disks with a recording time of half an hour per side were used to record complete protocols of our experiments.

RESULTS

The results here presented are drawn from 440 experiments on 149 animals. Not all these experiments were devoted to the study of gravity responses, as some preparations yielded responses to vibrational stimuli which form the subject of a separate publication. Of the recorded experiments, 40 on the utriculus, 26 on the sacculus, and 34 on the lagena yielded analysable results.

In the experiments on the response to gravity the skull was slowly tilted about a horizontal axis, the majority of the tilts being about the transverse or the longitudinal axes. The fore-and-aft tilts will be spoken of as 'towards Nose-up' or 'towards Nose-down' respectively, while the lateral tilts will be spoken of as 'Side-up' or 'Side-down'.

Utriculus

In most of the successful preparations a steady impulse discharge was observed when the nerve twig was connected to the amplifier. This steady discharge appears to be characteristic of labyrinthine sense endings (Lowenstein & Sand, 1940 *a*, *b*).

Example 1 (Text-fig. 3). Connexion to the amplifier was made in this case with the skull in the Upside-down position and a steady discharge at 6 impulses/sec. (20° C.) was picked up from a single fibre. The skull was tilted slowly and steadily towards the Nose-down position: the frequency of the discharge fell. The tilting was continued at constant speed and the discharge frequency reached a minimum near the Nose-down position, rising as the Normal position was approached. The rise was steepest within 20° of Normal becoming less steep near the Nose-up position in which the frequency of discharge reached a maximum. Tilting was continued through the Upside-down position to complete a second circle without a pause. Each full circle

occupied 2½ min. (2·4°/sec.). The discharge frequency fell as the Upside-down position was approached, being as low as 1/sec. on passing through that
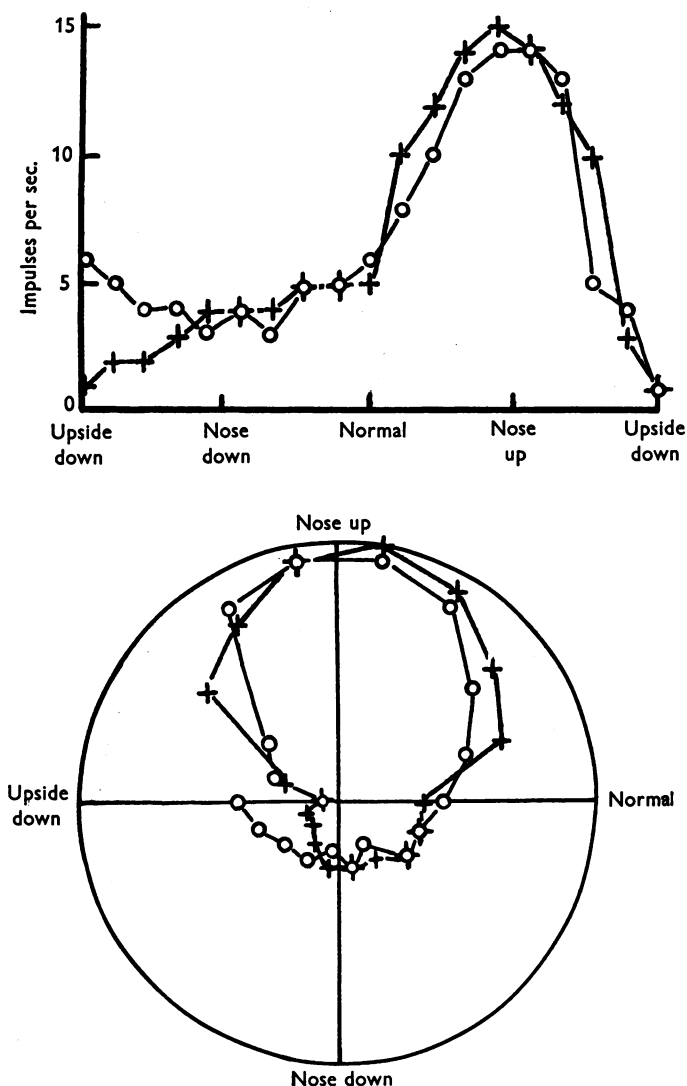
Text.-fig. 3. (Prep. 241.) Utriculus. Cartesian and polar graphs of the discharge frequencies during two consecutive full-circle fore-and-aft tilts. Both curves are to be read from left to right and counter-clockwise. O = first circle; + = second circle.

position. The discharge frequencies during the course of the second circle closely followed the frequencies found in the corresponding positions during the first circle. The skull was brought to rest in the Upside-down position after

the second circle and the discharge frequency rose within a few seconds to regain the steady value of 5/sec.
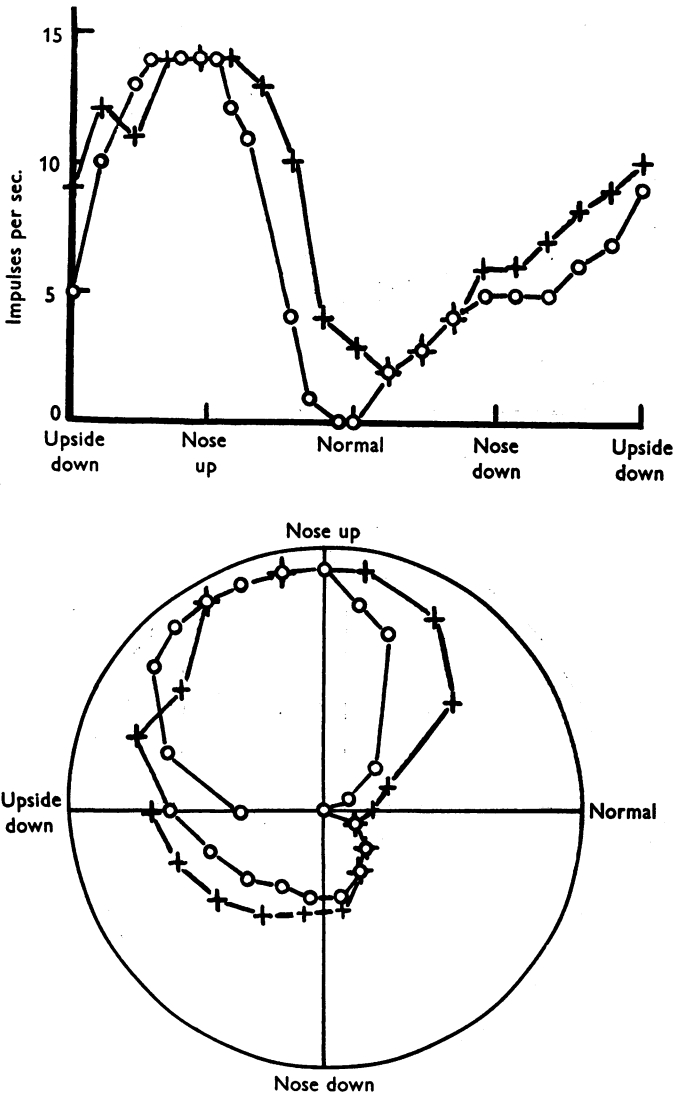
Text-fig. 4. (Prep. 241.) Utriculus. As Text-fig. 3. Both curves are to be read from left to right and clockwise. ○ =first circle; + = second circle.

A tilt was now carried out in the opposite direction, towards Nose-up, through two circles at the same constant speed without a pause (Text-fig. 4). The discharge frequency rose to a maximum at Nose-up, fell off towards Normal to a minimum between Normal and Nose-down, rising again towards

10/sec. in the Upside-down position. The frequencies found during a second circle agreed closely with the frequencies in the corresponding positions during
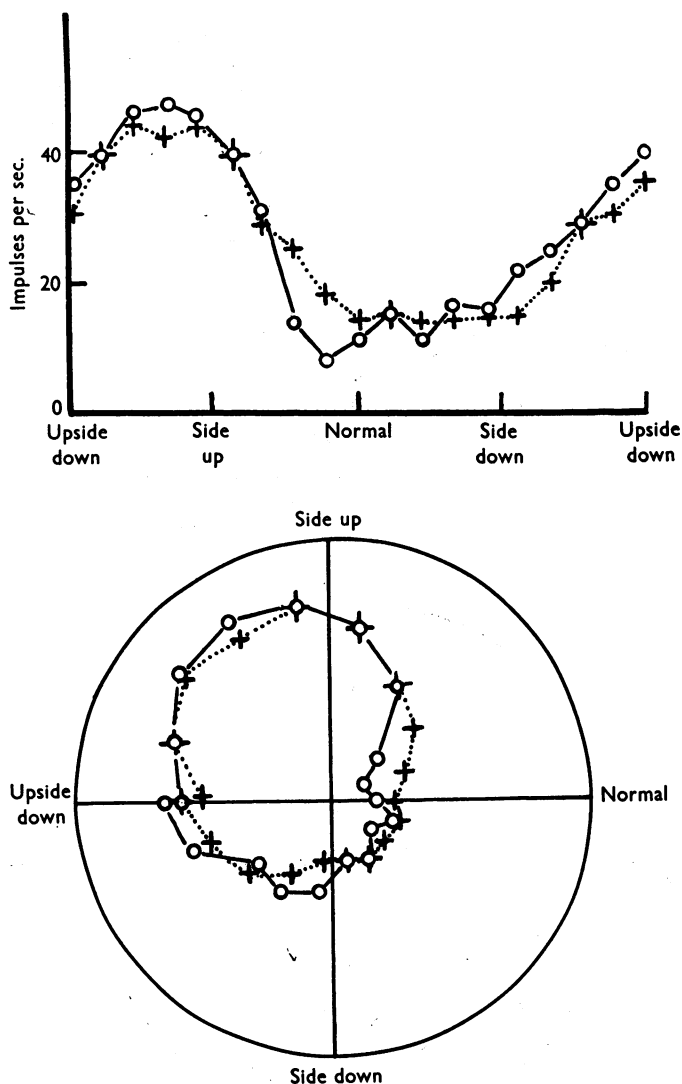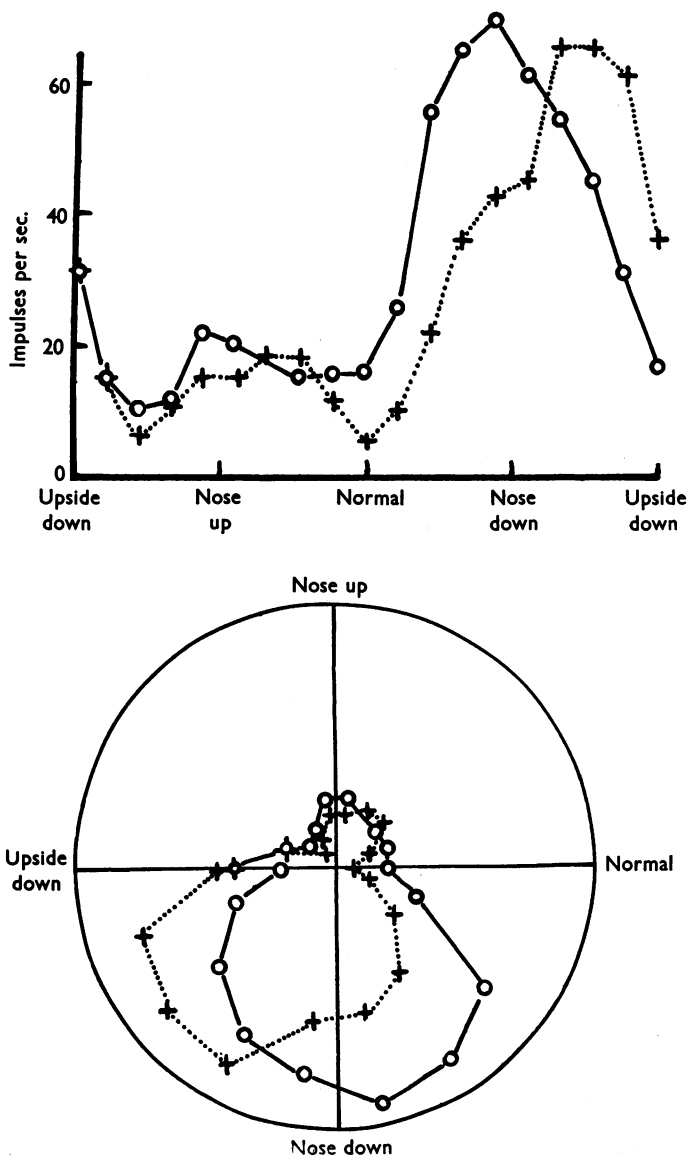

Text-fig. 5. (Prep. 286B.) Utriculus. The discharge frequencies during two full-circle lateral tilts in opposite directions. The continuous curves to be read from left to right and clockwise, the dotted curves from right to left and counter-clockwise.

the first circle. The agreement between the circles for the two opposite directions of turning was not quite so good.

Shortly after the skull had been brought to rest in the Upside-down position the discharge frequency fell to the value of 6/sec. characteristic of this position.

The skull was now tilted into the Nose-up position and held there. The discharge frequency rose to 16/sec. Within 30 sec. of the cessation of movement

Text-fig. 6. (Prep. 286 B.) Utriculus. The discharge frequencies during two full-circle fore-and-aft tilts in opposite directions. The continuous curve to be read from left to right and clockwise, the dotted curve from right to left and counter-clockwise.

in the Nose-up position the frequency had fallen to 11/sec., and it remained very close to this value for 20 min. At the end of this period the skull was
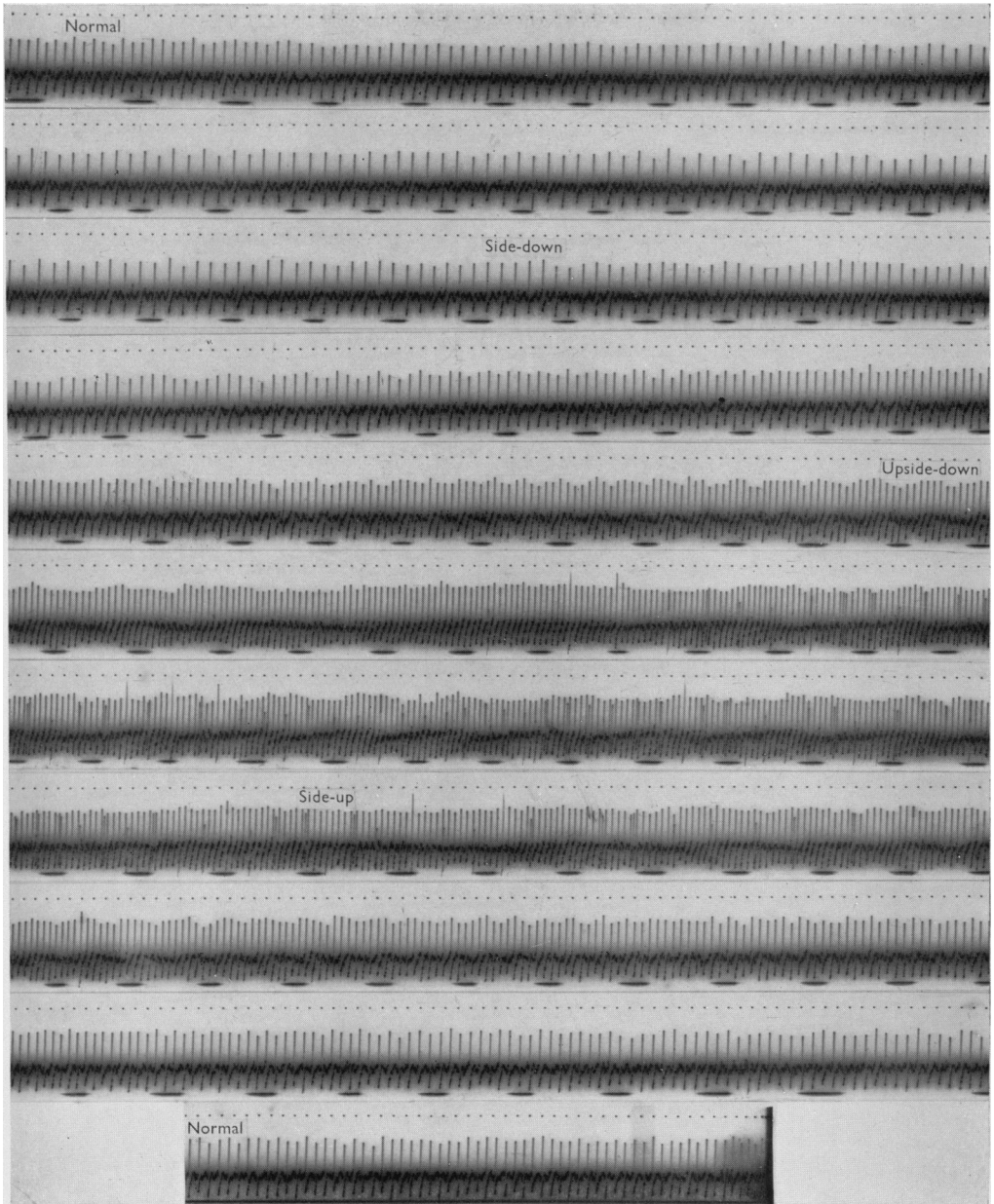
(Prep. 288.)   Utriculus: continuous film record of the response of a two-fibre preparation to a full-circle lateral tilt from Normal to Side-down to Upside-down to Side-up to Normal. Time marker at the top of record: 24/sec. Rotation signal at the bottom: one gap every 3°. Speed of rotation: 10°/sec. approx. The maximum discharge frequency lies near the Side-up and the minimum near the Side-down position.

returned to the Upside-down position, whereupon the discharge frequency returned to 6/sec.

A series of 360° tilts at different speeds was now performed. There was no significant variation of the response with the speed of tilting within the range 1·5°/sec. to 5·2°/sec. On lateral tilting this particular preparation did not show any significant alteration of discharge frequency. In this respect it is by no means representative. The majority of cases, including several preparations with only a single functional unit, showed a response both on fore-and-aft and on lateral tilting.

Example 2. Text-fig. 5 shows the response to lateral tilting of a 'few-fibre' preparation with a close agreement between the frequencies found in opposite directions of tilting. Text-fig. 6 shows the response of the same preparation to fore-and-aft tilting. It appears that the units contributing to the response in this case are of two types. One shows a maximum discharge frequency in a position near Nose-up, this position being independent of the direction of turning. The other shows its maximum near Nose-down, but the position at which this maximum is attained depends on the direction of tilting.

A similar dependence of the response on the direction of tilting was found in a large proportion of the preparations. The divergence between the maxima varied in extent. In some cases it was a few degrees only, whilst in others the maxima lay in opposite quadrants (Text-fig. 8).

Example 3. This preparation showed a moderate divergence in the position of the maximum both on lateral tilting and on fore-and-aft tilting. It was a two-fibre preparation in which one unit was preponderant and lent itself to separate quantitative analysis (Pl. 1). It should be noted that the unit having the smaller amplitude was inactive over a considerable part of the full circle. Apart from this the spatial characteristics of its response are similar to those of the pre-dominant unit. Tests were also carried out with the preparation stationary in a series of positions 45° apart all round the fore-and-aft and lateral circles. The change from one position to the next was carried out very slowly, and readings of the discharge frequency were taken after the preparation had been at rest for 30 sec. Text-fig. 7 shows the relation between the steady frequencies in the various positions and the frequencies attained during continuous smooth tilts in two directions. A precisely analogous result was obtained on fore-and-aft tilting.

Example 4. In this preparation the divergence between the position of the maxima on opposite directions of tilting is as great as has been found in any preparation (Text-fig. 8). In the experiment illustrated by this figure, tilting started from the Normal position. Another experiment on the same preparation, starting in the Upside-down position, gave very similar figures. Lateral tilts were also performed starting both from Normal and Upside-down, and we were satisfied that the initial position has no significant effect on the character of

the full circle response, which depends, in this case, only on the direction of tilting.
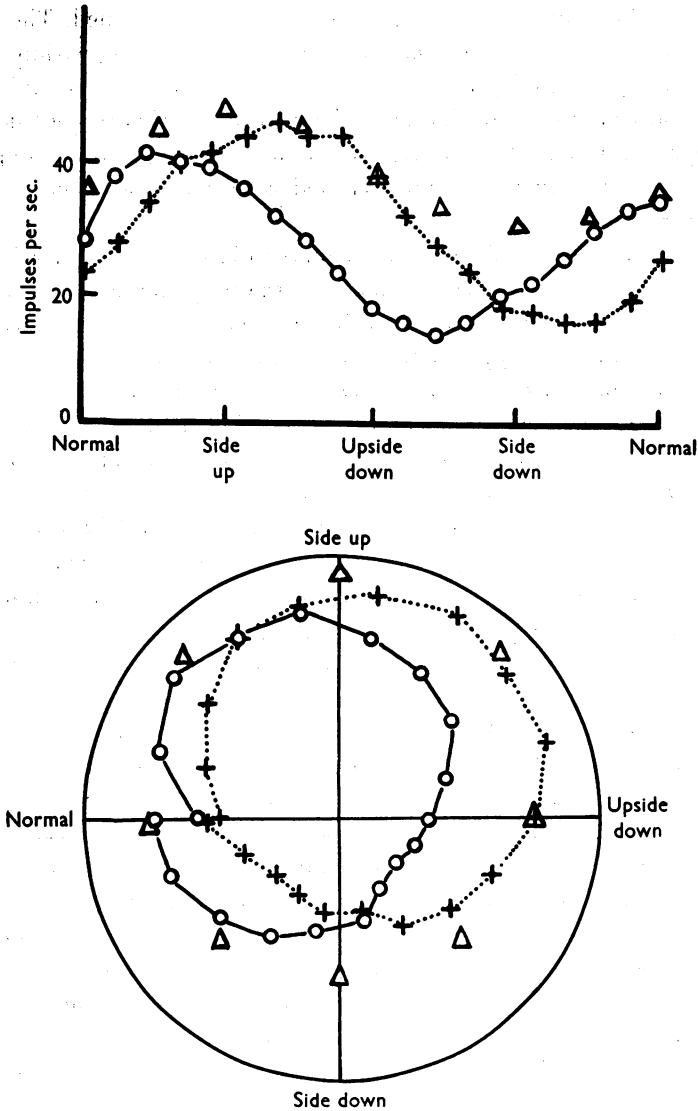
Text-fig. 7. (Prep. 288.) Utriculus. The discharge frequencies of two full-circle lateral tilts in opposite directions. The continuous curve to be read from left to right and clockwise, the dotted curve from right to left and counter-clockwise. The superimposed frequency readings marked △ were taken during an interrupted full-circle tilt after 30 sec. rest in each position.

With this preparation also tests were made of the relation between the frequencies found during continuous turns and those found in various positions after the preparation had been held stationary. A very slow rotation was

carried out (45° in 30 sec.), interrupted every 45° by a stationary period lasting 1 min. Text-fig. 9 shows the frequency readings at the beginning and at the
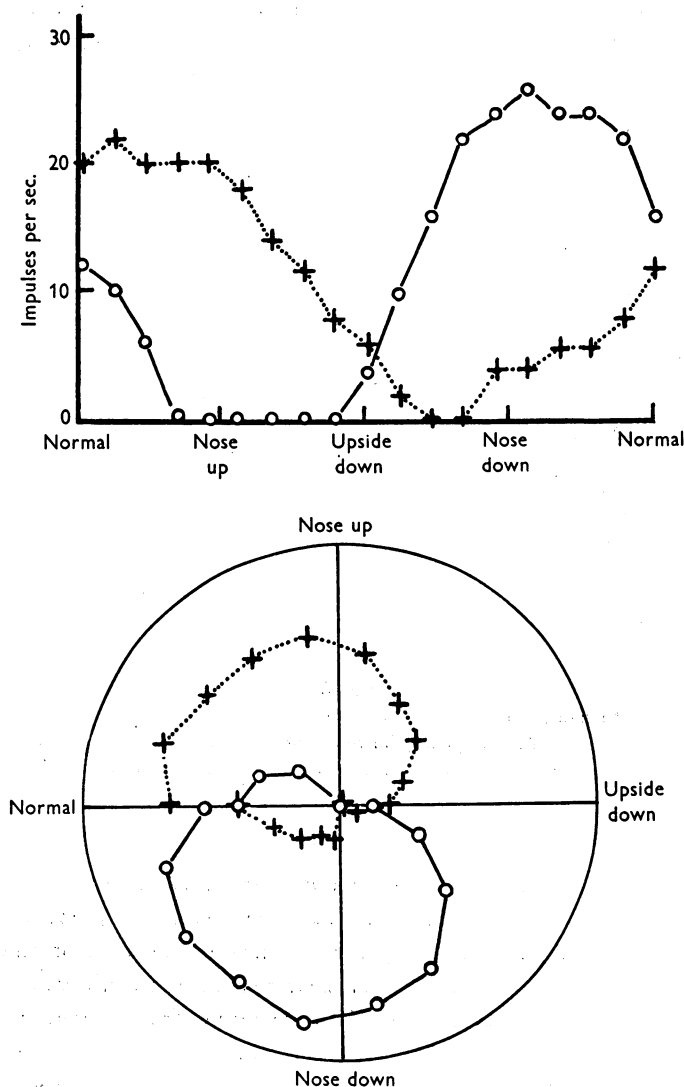
Text-fig. 8. (Prep. 249.) Utriculus. The discharge frequencies during two full-circle fore-and-aft tilts in opposite directions. The continuous curve to be read from left to right and clockwise, the dotted curve from right to left and counter-clockwise.

end of the stationary periods. For comparison the plottings are superimposed upon a curve of the frequency trends during a more rapid uninterrupted full circle tilt. It is clear that the discharge frequency returns in every case to a basic level and that it therefore is unsuitable to furnish a position signal. In

a preparation of this type it was also interesting to see the response to tilting about axes intermediate between the longitudinal and transverse axes. Tests about the two axes at 45° from the longitudinal gave results similar in type to those illustrated in Text-fig. 8 but with a smaller divergence between the maxima.
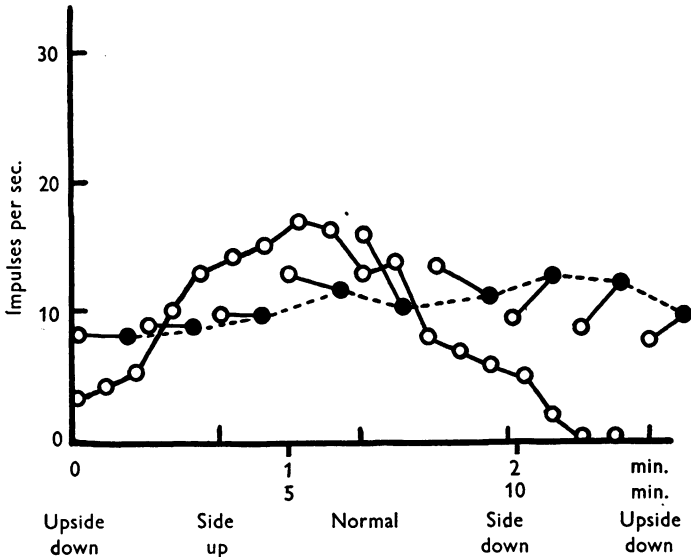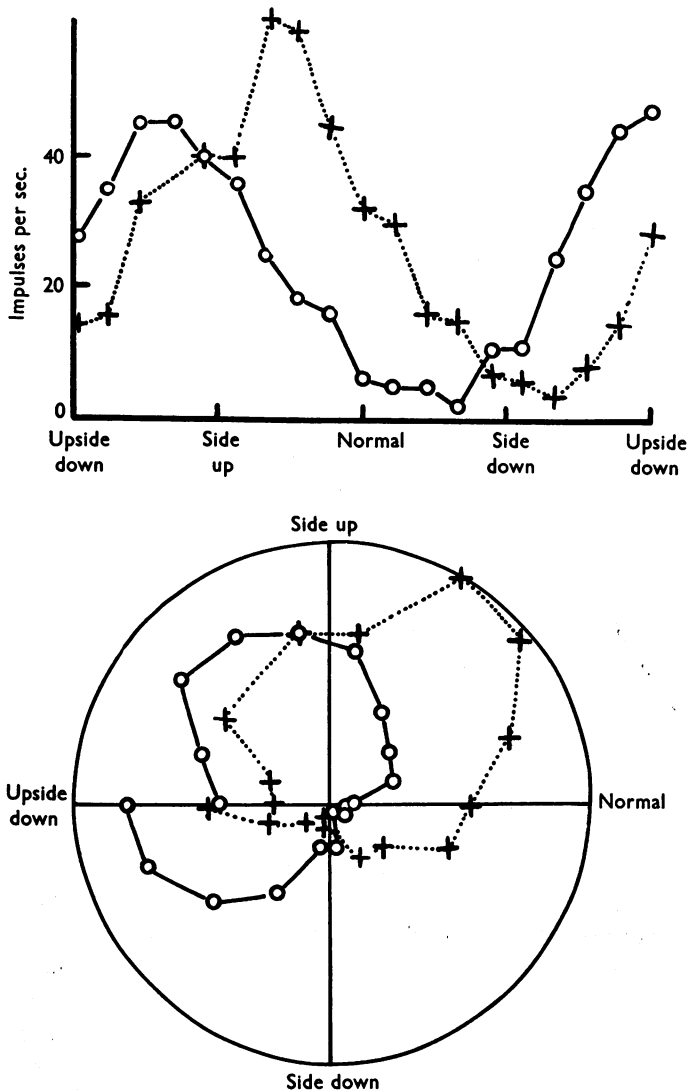

Text-fig. 9. (Prep. 249.) Utriculus. The discharge frequencies during a full-circle lateral tilt, to be read from left to right. Superimposed are the frequency readings during an interrupted tilt in the same direction. ○ =frequency on reaching position, ● =frequency after 1 min. rest in position. The latter readings are connected by a dotted line to show 'basic' discharge level.

Sacculus

In the light of the results of previous workers (Lowenstein, 1936) it would not have been surprising to find the sacculus devoid of gravity responses. This expectation has been fulfilled for a considerable area of the sacculus macula, preparations of which showed clear responses to vibrations but were not influenced by positional changes. Results gained from preparations of this type will be dealt with in a separate publication.

In each preparation in which a rotation response could be observed it took the form of a modification of a resting discharge as described for the utriculus. Despite certain difficulties which arise in the localization of a particular end-organ within a given macula (to be discussed later), it is clear that in the anterior two-thirds of the macula of the sacculus vibration receptors preponderate over gravity receptors, whereas in the posterior region the reverse is the case. The character of the responses is in some cases very similar to that found in the utriculus.

Example 5. Text-fig. 10 shows the response to lateral tilting in two directions of a 2- to 3-fibre preparation. During a second circle in each direction the

Text-fig. 10. (Prep. 269 A.) Sacculus. The discharge frequencies during two full-circle lateral tilts in opposite directions. The continuous curves to be read from left to right and clockwise, the dotted curves from right to left and counter-clockwise.

sequence of discharge rates (not shown in the figure) closely followed that found during the first circle. It will be seen that the response in this case resembles the utricular response shown in Text-fig. 7.

Example 6. In another preparation lateral tilting produced a response of a type essentially similar to that illustrated by Text-fig. 5 for the utriculus.

The results from the sacculus thus display a range of response types similar to that described for the utriculus. Preparations showing a maximum discharge frequency in or near the Nose-down position appeared to predominate in the sacculus, whereas in the utriculus maxima in or near the Nose-up position were more frequently encountered. Preparations showing maxima near the Side-down position were equally rare in both organs.

In preparations of the type so far described the change in discharge frequency is continuous throughout the full-circle rotation. The response of some receptors, however, is limited to a part only of the full circle, the discharge frequency remaining steady during the rest of the circle, sometimes for more than 180° of tilting. In such cases the response may appear as a series of 'bursts', each persisting for only a short range of tilting (10–40°). The bursts do not occur at the same positions in successive circles, and for this reason we have come to the conclusion that these latter preparations may not be representative of the natural behaviour of the sense-organ.

The sacculus does not differ materially from the utriculus in its capacity for signalling maintained displacements by characteristic discharge frequencies.

Lagena

The most striking features of the behaviour of the lagena are the uniformity of the response patterns obtained and the complete freedom from vibration sensitivity.

Example 7. Text-fig. 11 shows the response of a single functional unit during a lateral tilt from Side-down to Side-up through Normal. It will be seen that the maximum is comparatively sharp and that it occurs near the normal position.

This behaviour is typical of most of the preparations observed, and the deviations of the maximum from the Normal position in these cases are generally less than 30°. The discharge frequencies in various positions are, in these typical cases, independent of the direction of tilting. A similar discharge pattern is obtained on fore-and-aft tilting; here, too, the discharge frequency rises steeply as the normal position is approached from either direction.

In some preparations with more than one functional unit, a second (usually smaller maximum occurred near the Upside-down position (Text-fig. 13). We have no evidence as to whether such a second maximum can occur in the response of a single unit.

A considerable number of sense endings in the lagena are silent for more than 180° of tilting, becoming active in rapid succession on approaching the Normal position. In consequence, a preparation which in the Upside-down position has the appearance of containing only a single unit may, in the Normal

position, show a massive discharge of very high frequency. *Example* 8 (Text-fig. 12) shows such a response picture. Some preparations have been obtained
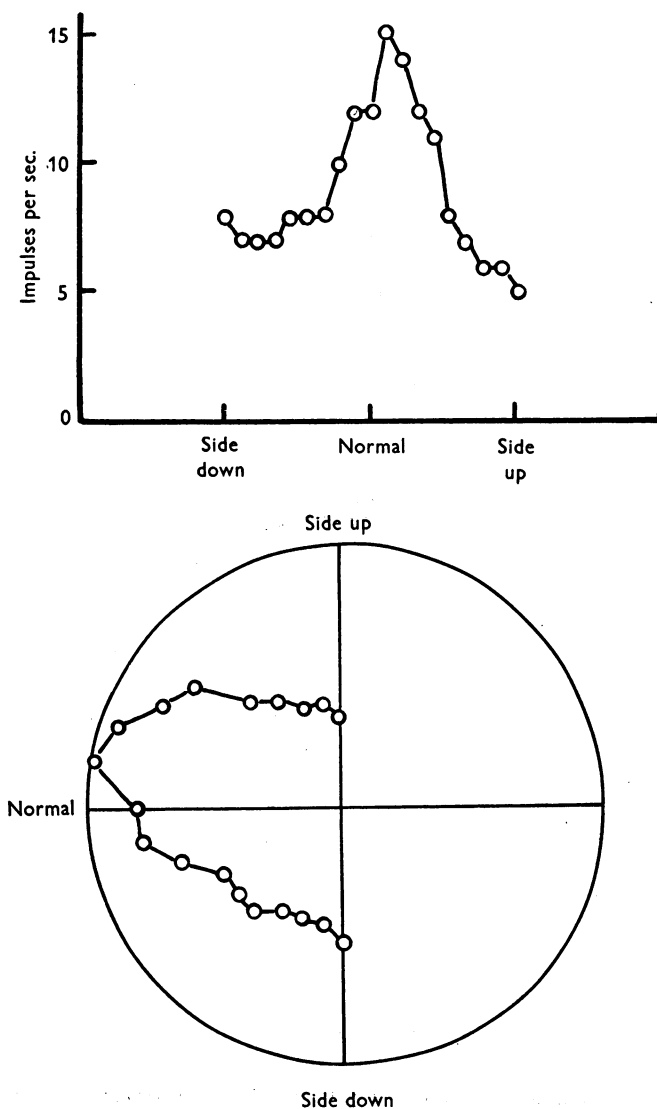
Text-fig. 11. (Prep. 129.) Lagena. The discharge frequencies during a 180° lateral tilt. To be read from left to right and clockwise.

in which the maximum discharge frequency occurs in different positions according to the direction of tilting. *Example* 9 (Text-fig. 13) shows such a response from a few-fibre preparation to fore-and-aft tilting in two directions.

Example 10 (Text-fig. 14) shows the relation between the discharge frequencies
in various positions during a smooth tilt and those found while the preparation
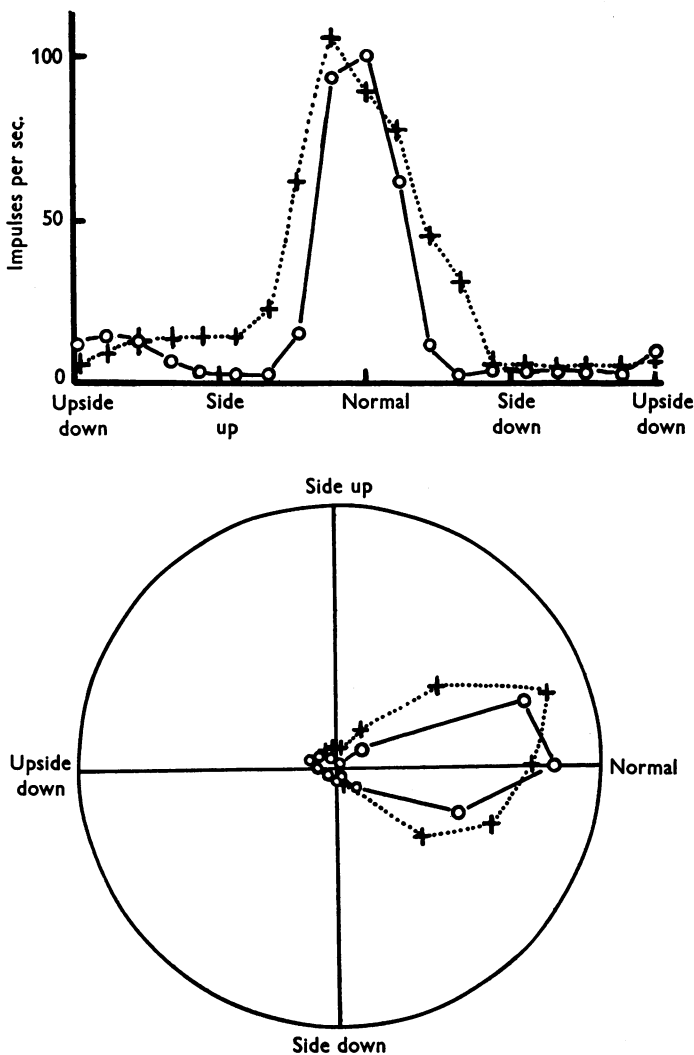
Text-fig. 12. (Prep. 213.) Lagena. The discharge frequencies during two full-circle lateral tilts. The
continuous curves to be read from left to right and clockwise, the dotted curves from right to
left and counter-clockwise.

was held stationary in the corresponding positions for 3 min. It is clear from
this experiment that the lagena, too, contains sense endings which satisfy the
requirements for positional receptors.
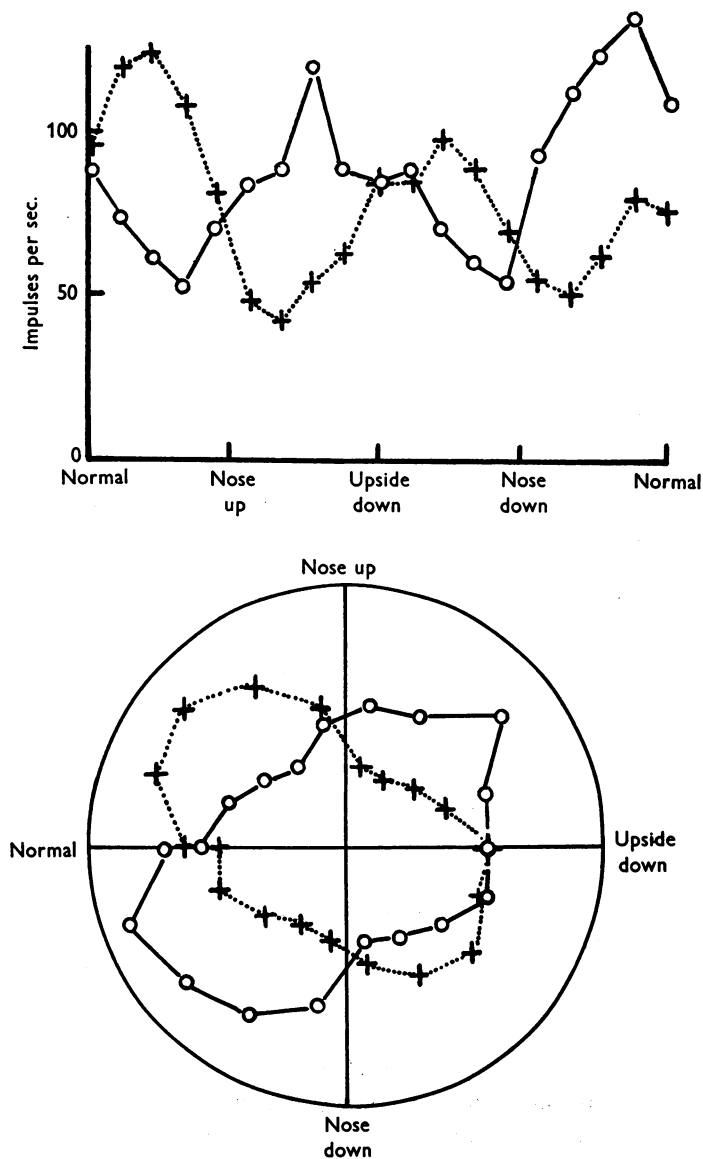
Text-fig. 13. (Prep. 76.) Lagena. The discharge frequencies during two full-circle fore-and-aft tilts. The continuous curves to be read from left to right and clockwise, the dotted curves from right to left and counter-clockwise.

Responses to linear translations

Tests were finally carried out with the object of recording the responses of the gravity receptors in the otolith organs to linear translations. As we had no provisions for the application of quantitatively controlled stimuli of this kind

the tests were improvised and qualitative only. The preparation holder held in the hand of the operator was moved forwards and backwards, from side to side, and up and down. The absence of signals made it impossible to subject the photographic records to an accurate analysis. It was, however, clear that increases and decreases in the discharge frequency occurred on opposite movements, and that an increased discharge appeared to be correlated with inertia movements of the otolith mass away from the macula and vice versa. For technical reasons no tests could be carried out for responses to centrifugal force. The existence of such reactions must, however, be postulated in organs designed to respond to linear accelerations.
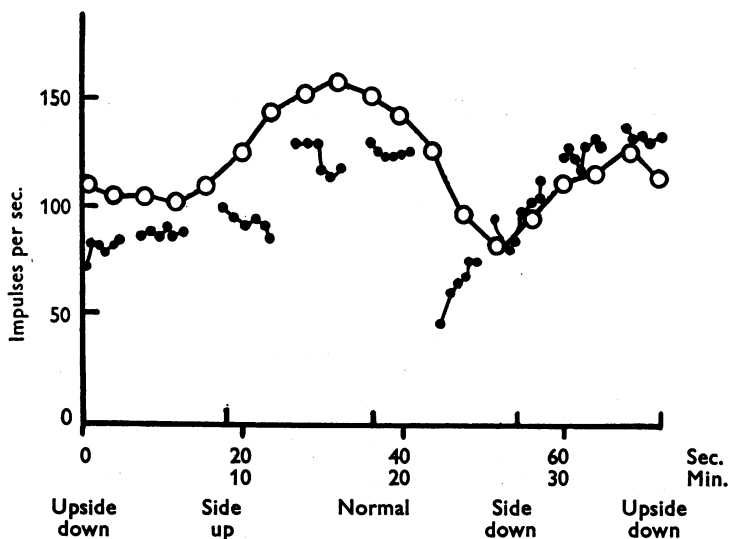
Text-fig. 14. (Prep. 227.) Lagena. The discharge frequencies during a full-circle lateral tilt, to be read from left to right. ○ =frequency readings during continuous tilt (time scale, sec.), ● =frequency readings with preparation at rest in different positions (time scale min.).

DISCUSSION

In the labyrinth of the ray all three otolith organs, viz. utriculus, sacculus, and lagena participate in the maintenance of equilibrium. This result, although in full agreement with the classical conception of labyrinth function, may be considered surprising in the light of relatively recent work on a number of different vertebrate types ranging from bony fishes to mammals, where elimination of the sacculus or the sacculus-lagena complex did not significantly affect any of the known labyrinthine reflexes (Lowenstein, 1936). Considering the phylogenetic position of the Elasmobranchs, however, it is highly interesting to find in a member of this group the generalized functional picture represented by our results. Breuer (1891) postulated in his classical theory of otolith function a division of labour between the otolith organs in which their range of

response, like that of the semicircular canals, was strictly correlated with their anatomical arrangement with respect to the three main planes of space. Our results do not bear this out. There is a wide overlap in functional range between the otolith organs, as their sense-endings were generally found to respond to tilts about both the longitudinal and the transverse axis. Adrian (1943) reports a similar behaviour of some of the gravity-controlled units in the brain stem of the cat. The lagena does show a typical response picture of its own, but this bears no relation to Breuer's speculation, and owing to its absence in mammals the organ plays no part in the later functional theories put forward by Quix (1925) and Magnus & de Kleijn (1926 *a*, *b*).

It is clear from the similarity in response from the utriculus and the sacculus that, during deviation from the normal position, a considerable number of receptor units in both organs must be sending almost identical and thus mutually reinforcing signals to the central nervous system. It may, therefore, be permissible to assume that either of the two organs could phylogenetically be switched to another task, such as vibration reception, without depriving the labyrinth of any specific category of gravity reception. This appears, in fact, to have happened several times in vertebrate evolution. The bony fish represent a good example. In the Cyprinoids there is strong evidence that the sacculus and lagena complex can be eliminated without any noticeable effect on equilibration (Lowenstein, 1932). A remarkable capacity for hearing and sound discrimination was shown to be localized in this part of the labyrinth (v. Frisch, 1936). In the Clupeids there are strong indications that the acoustic function of the ear may have its main seat in the utriculus, and the possibility cannot be ruled out that here the sacculus may be the chief equilibrium organ among the otolith-bearing structures of the labyrinth (de Burlet, 1935).

The vibration sensitive sense-endings in the elasmobranch labyrinth are found in the utriculus (lacinia), in a large part of the sacculus macula, and in the macula neglecta. These results will be presented in a separate paper in this *Journal*. The macula lagenae is wholly made up of gravity receptors. The phylogenetic fate of this sense-ending is interesting. In some bony fish it is probably concerned with hearing. In Amphibia its loss was claimed by McNally & Tait (1925) to be without effect on equilibrium, but it has now been shown by MacNaughton & McNally (1946) that the unilateral loss does bring about a deficiency pose of the head consisting of slight homolateral upward tilts, whereas the only consequence of bilateral elimination of the lagena is oscillation of the head on coming to rest after spontaneous movement, which amounts to a deficient stabilization of the head near the normal position. Possession of the lagenae after elimination of all other labyrinthine sense-endings preserves a prompt righting reflex absent in animals after total bilateral labyrinth elimination. These findings in the Amphibia agree well with the responses recorded from the elasmobranch labyrinth, which show the

lagena as a marker for the normal position. It is tempting to speculate, that the gravity responses recorded by Ross (1936) from the ramus inferior of the eighth nerve of the frog may have been derived from the lagena. In birds the lagena becomes separated from the sacculus by its close association with the tip of the cochlear outgrowth, and in mammals it is missing altogether. A gradual loss of equilibrium function and, probably, association with sound perception precedes its final disappearance. It is thus quite clear that the otolith organs show great functional plasticity, their potentialities being fore-shadowed in the generalized conditions obtaining in the elasmobranch labyrinth.

A question of great interest in the study of a 'stato-receptor' is whether it is capable of signalling persistent deviations from the normal spatial orientation. Theoretically one would expect such a receptor to have a characteristic dis-charge rate for every position, or at least for a number of critical orientations. Sense-endings approaching this ideal type are represented by examples illustrated in Text-fig. 7 (utriculus) and Text-fig. 14 (lagena). They have also been found in the sacculus. When in such a case the preparation is very slowly tilted from Normal to a certain position in space, the frequency of discharge increases or decreases. When the preparation is then held stationary in the 'abnormal' position the increased or decreased discharge frequency reverts somewhat towards the initial level, remaining, however, significantly above or below it for a matter of minutes.

Prejudiced by the universally accepted prototype of a 'stato-receptor' we were somewhat surprised to find that a considerable proportion of the sense-endings in the three maculae did not show this capacity to signal, in this way, maintained deviations from the normal spatial position. An extreme case of this type is illustrated by Text-fig. 8 (utriculus). This receptor shows a marked fall in activity whenever the normal position is left, moving towards a minimum irrespective of whether the labyrinth is lowered or raised. After transit through the Upside-down position its activity rises towards a maximum, whatever the direction of rotation. Text-fig. 9 shows that the activity reverts to a basic level whenever the tilt is interrupted for any length of time. Such a receptor cannot by any stretch of imagination be called a 'stato-receptor'. It is, how-ever, suited to signal positional change as such, and may be described as an out-of-position receptor. The semicircular canals fulfil a similar task. But they react to angular accelerations only, whereas the gravity-controlled out-of-position receptors respond to constant-speed spatial deviations.

In yet another respect our results are in evident contradiction to the hitherto generally accepted model of otolith function. The effect of unilateral total labyrinthectomy in all vertebrate classes is primarily a loss of anti-gravity tonus on the operated side which leads to the well-known rolling over to this side during forward progression. As this tonus asymmetry is accentuated by

a tilt to the normal position, and is least noticeable when the animal comes to rest lying on its operated side, the conclusion was naturally reached that the otolith organ responsible for the perception of lateral tilts is maximally stimulated when the labyrinth is lowered. The findings of Tait & McNally (1934) in what they call the uni-soliutricular frogs, in which all labyrinthine receptors except one utriculus were eliminated by nerve cutting, also point towards ipsilateral preponderance of the anti-gravity muscles under the influence of the intact vestibular end organ. In agreement with this, all records obtained from the vestibular nucleus of the mammalian brain stem (Adrian, 1943) show increased impulse discharge on side-down tilting, which has been tentatively attributed to the activity of the ipsilateral sacculus. Consequently, we expected to find that at least a majority of sense-endings in the utriculus or sacculus, or both, increase their discharge frequency on side-down tilting. The opposite is the case. We are inclined to believe that the regions of the maculae from which we recorded were fairly representative of the whole; yet all sense-endings capable of signalling maintained deviations from the Normal showed a decreased activity in or near Side-down, and conversely a maximum in or near Side-up positions.

The explored parts of the utriculus and sacculus maculae contain at least two types of sense-endings, one responding with an increase in discharge to Side-up and Nose-up, the other to Side-up and Nose-down displacements. Nerve fibres from these two types can be found side by side in one and the same nerve twig. This does not, however, mean that they are necessarily derived from neighbouring neuromasts, as a considerable amount of fanning-out is characteristic of the end-ramifications of the nerve strands. It is thus difficult to localize the exact position of the sense-endings concerned with sufficient confidence to justify far-reaching theoretical deductions. From the fact, however, that the lateral parts of the utriculus macula yield preponderantly preparations whose discharge frequency increases on Side-up tilting, it may be tentatively suggested that either a gliding away of the otolith, producing a medial deflexion of the sense hairs of the neuromasts or a relief of the vertical pressure of the otolith on the macula, may represent the appropriate stimulus, with the reverse hair deformation or pressure change producing a reduction in the discharge frequency. If this were correct then the Side-up and Nose-up organs ought to be located in the antero-lateral, the Side-up and Nose-down organs in the postero-lateral part of the utriculus macula. This localization would be in full agreement with the stimulation experiments on the dogfish (Maxwell, 1923) where it was found that pressure on the otolith applied laterally, so as to move the otolith slightly inwards, produced eye responses corresponding to those occurring on the lateral up-tilting of the stimulated labyrinth. Pressure on the anterior side of the otolith produced the effect of Nose-up tilting, and pressure on the posterior end the opposite. From this
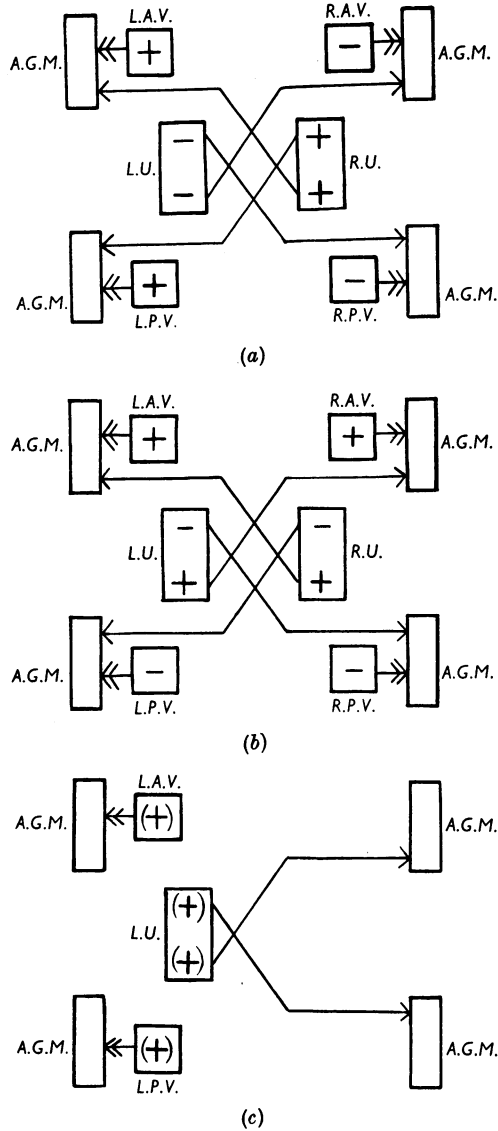
Text-fig. 15. Diagrammatic representation of the hypothetical tonus-distribution from vertical canals and gravity receptors to the anti-gravity muscles of the four limbs: (*a*) during lateral tilt to the left; (*b*) during Nose-down tilt; (*c*) in the normal position after elimination of the right labyrinth. *A.G.M.* = anti-gravity muscles; *L.A.V.* = left anterior vertical canal; *L.P.V.* = left posterior vertical canal; *L.U.* = left utricle; *R.A.V.* = right anterior vertical canal; *R.P.V.* = right posterior vertical canal; *R.U.* = right utricle. The + sign denotes an increase, the − sign a decrease in the discharge frequency during tilting movements. (+) indicates the tonus effect of the resting discharge in the stationary labyrinth. All four vertical canals would be marked (+) in the absence of angular acceleration. The double arrow-head from the canals symbolizes their assumed preponderance (see text).

Maxwell concluded that the effective stimulus is a displacement of the otolith. This satisfactory agreement based on two entirely different methods is not supported, however, by the results of similar stimulation experiments on the pike (Ulrich, 1935). Here the effects of delicately apportioned pressures on the utriculus otolith are directly opposed to those described by Maxwell.

If any permanent association between certain macula areas and groups of effector muscles existed, this would mean that the utriculus and sacculus maculae in a tetrapod are preponderantly in control of the contralateral anti-gravity muscles, with the anterior and posterior parts of the maculae controlling the posterior and anterior pairs of limbs respectively (Text-fig. 15). It will be seen from the diagrammatic representation of this hypothetical scheme that the otolith organs are assumed to be antagonistically pitted against the vertical canals spatially associated with them. Text-fig. 15 *a, b* illustrate the distribution of excitation on a left Side-down and a Nose-down tilt, with the plus and minus signs indicating increased and decreased discharge-activities respectively. The apparent discrepancy between the deficiency phenomena found after unilateral total labyrinth elimination and our electro-physiological findings can be overcome by making the additional assumption that the sum total of the tonic influence of the semicircular canals, apart from being opposed to that of the otolith organs, is also significantly stronger. Such an assumption would lead back to Ewald's theory of the 'tonus labyrinth' in which the canals were described as the chief source of labyrinth tonus. Text-fig. 15 *c* illustrates the distribution of excitation after total elimination of the right labyrinth, and it will be seen that the typical deficiency phenomena based on tonus preponderance on the intact side can be readily deduced from it. Although it is very tempting to adopt some such *ad hoc* scheme of explanation, it must be said that the pattern of functional integration is probably more complicated. A significant indication that this may be so, is the fact that Tait & McNally (1934), in their interpretation of elimination experiments on the frog's labyrinth, found themselves forced to abandon the prevailing idea that the otolith 'acts by a simple and uniform sliding descent from a higher to a lower level' and came to the conclusion that a 'hypothesis of a point-to-point independence of the elements composing the otolith organs is unavoidable'.

A central projection of the 'macula map' as a whole may be assumed to furnish the substrate for a side-by-side and moment-to-moment representation of the sum total of deformation effects in the maculae, with the effector system reacting to the stimulus situation as a whole rather than to discrete aspects of it. Such a picture would be very acceptable, if it did not by its very nature defy experimental analysis. But this is a difficulty common to a number of sensory fields.

SUMMARY

1. In the labyrinth of *Raja clavata* all three otolith organs, viz. the utriculus, sacculus, and lagena participate in the maintenance of equilibrium.

2. Sense-endings in the maculae generally show a resting discharge, the frequency of which is increased or decreased by positional changes.

3. The functional ranges of utriculus and sacculus overlap. Both contain sense-endings responding to lateral and fore-and-aft tilting. There are two main types which have their maximum of discharge activity in Side-up and Nose-up and Side-up and Nose-down positions respectively. Organs having a maximum in the Side-down position were encountered, but did not appear among the position-receptors proper.

4. Apart from 'static' position receptors, the maculae contain receptors responding to a change of position in one and the same manner, irrespective of the direction of the change. They are described as 'out-of-position' receptors.

5. The receptors in the lagena also respond both to lateral and to fore-and-aft tilts. They have their maximum of activity usually in or near the normal position and can be described as 'into-level' receptors.

6. The otolith organs show clear reactions to linear translations in the three planes of space. These, and theoretically postulated reactions to centrifugal force, have not yet been subjected to a quantitative analysis.

7. The theoretical implications of the electro-physiological findings are discussed.

REFERENCES

Adrian, E. D. (1943). *J. Physiol.* **101**, 389.
Breuer, J. (1891). *Pflüg. Arch. ges. Physiol.* **48**, 195.
Burlet, H. M. de (1935). *Acta oto-laryng., Stockh.,* **22**, 287.
Ewald, J. R. (1892). *Physiologische Untersuchungen über das Endorgan des Nervus Octavus.* Wiesbaden: Bergmann.
Frisch, K. von (1936). *Biol. Rev.* **11**, 210.
Lowenstein, O. (1932). *Z. vergl. Physiol.* **17**, 806.
Lowenstein, O. (1936). *Biol. Rev.* **11**, 113.
Lowenstein, O. & Sand, A. (1940*a*). *J. Physiol.* **99**, 89.
Lowenstein, O. & Sand, A. (1940*b*). *Proc. Roy. Soc.* B, **129**, 256.
McNally, W. J. & Tait, J. (1925). *Amer. J. Physiol.* **75**, 155.

MacNaughton, I. P. J. & McNally, W. J. (1946). *J. Laryng.* **61**, 204.

Magnus, R. & Kleijn, A. de (1926a). *Handb. norm. path. Physiol.* Band **11**, p. 868. Berlin: Springer.

Magnus, R. & Kleijn, A. de (1926b). *Handb. norm. path. Physiol.* Band **11**, p. 1002. Berlin: Springer.

Maxwell, S. S. (1923). *Labyrinth and Equilibrium.* Philadelphia and London: Lippincott.

Quix, F. H. (1925). *J. Laryng.* **40**, 425.

Ross, D. A. (1936). *J. Physiol.* **86**, 117.

Tait, J. & McNally, W. J. (1934). *Philos. Trans.* B, **224**, 241.

Ulrich, H. (1935). *Pflüg. Arch. ges. Physiol.* **235**, 545.